II. *On the Formation of the Cells of Bees and Wasps.*
By G. R. WATERHOUSE, F.Z.S., &c.

[Read 7th March, 1864.]

AT a former meeting of this Society, a discussion having arisen respecting the theory of the structure of the cells of wasps, &c., I stated that I possessed the commencement of a hornet's nest—or rather of the *comb*—in which there were but three cells, and these only partially built: that these cells were so placed that each one came in contact with two others, and had two flat sides, the flat sides forming the common partitions between two cells; and that the remaining portion of each cell (being about two-thirds of the entire circumference) was circular at the opening.

I promised to exhibit this rudimentary condition of a hornet's nest, and was reminded of this promise by our ex-President at the last meeting. I now lay it before you (Pl. XIII. figs. 1 and 1*a*); but before I proceed to make any remarks respecting it, I am anxious to direct the attention of the members to other nests and cells of Hymenopterous insects; and especially to the very extensive collection of these interesting objects exhibited in the small room at the east end of the northern Zoological Gallery of the British Museum. Here will be found between three and four hundred nests of various kinds of bees, wasps, &c. These nests, and many others which I have had opportunities of examining, may be divided into three principal classes.

I. Nests formed in burrows in the ground, or in dead wood. They are very numerous, and the cells of which they are composed are either cylindrical or ovate, sometimes round, or nearly so.

II. Isolated cells, not deposited in such excavations, but merely attached to some foreign substance. They are frequently ovate, sometimes cylindrical and sometimes spherical—never angular.

III. Groups of cells more or less closely united, not deposited in excavations or burrows, but either attached to some foreign substance, or to a nest-covering made by the insects. Here the form of the cell is commonly hexagonal.

Now it is a striking fact that of these different kinds of nests (aggregates of cells) or isolated cells, both groups of insects mentioned—bees and wasps—furnish all the different varieties above noticed. Bees and wasps, we must bear in mind, form two very extensive and distinct sections of the order *Hymenoptera*, distinguished by many important points of structure. Each of these great sections is divided into families and genera, also characterized by differences of structure. Here then are insects of two distinct great sections furnishing repetitions of similar architecture in the construction of their nests and cells; on the other hand, we find instances of species of the same genus building nests and cells which are very dissimilar, not only as to the structure, but as to the material used. In short, insects, very dissimilar in form and structure, build similar nests and cells, and insects of (*very nearly*) the same form and structure build dissimilar nests and cells. From this we may infer, either that the influence of the form and structure of the insect upon that of the nest and cell must be but of minor importance; or, that the differences in the structure of the nests and cells are more apparent than real. I entertain the latter idea, and nearly thirty years back, when called upon to write the article "*Bee*" for the Penny Cyclopædia, I endeavoured to show that there was a common principle in action in all insect architecture, viz., that of working in segments of circles; and that, so far as the hive-bee was concerned, the cells of that insect furnished no exception to the rule.

The theory propounded by me, in explanation of the form of the cell of the hive-bee, has been objected to by several able naturalists, since it will not serve likewise to explain the hexagonal form of the cell of the wasp or hornet, it being surmised that the same laws would govern the form of the cell in both cases.

In 1835, when I wrote the article alluded to, I was not acquainted with certain facts relating to the building of the wasp's nest, and when I learnt that a single female wasp constructed, in the spring time, a nest made up of hexagonal cells, I felt that the objection that had been raised against my views was a very serious one.

The leading idea with me, in respect to the cells of the honeycomb, was that of a number of insects working simultaneously (or nearly so) in a confined space; but, with the wasp, the case is different, and in fact, as I soon afterwards discovered, is precisely the reverse; for it is a single insect, in unconfined space, working simultaneously (or very nearly so) at many cells: that is, so far as the nest first formed by the female wasp is concerned. The cells constructed later in the season by the neuter wasps, I have no doubt, come into the same category as the cells of the hive-bee.

Having made these preliminary remarks, I will now direct your attention to one or two other specimens which I have to exhibit. But first I wish you to observe, with regard to the specimen of part of a nest already exhibited, that it consists of a stalk by which it was attached to the nest-covering, the stalk being slender in the middle and expanded at the extremities—at the base to increase the surface for attachment, and at the opposite extremity to unite with the three cells. Viewing this specimen from the side, or with the stalk towards you, there is no trace of plane surfaces; all the work is in curves, and the partially formed cells appear to be hemispherical. It is only when you view it with the openings of the cells towards you that plane surfaces are visible, and these are presented by the flat partitions between the cells. You will also perceive that were the now partially circular outline of the opening of one of these cells to be carried on and completed, it would encroach upon the two neighbouring cells.

This specimen originally formed part of an enormous hornet's nest, the nest consisting, as usual, of a number of horizontal slabs composed of cells, and a thick covering enclosing the whole and constructed of the same materials as the cells. The covering, in parts, was very irregular, no doubt arising from the situation in which the nest was placed (most probably in a hollow tree). On its inner surface were many small cavities, in several of which were small rudimentary nests, or rather portions of comb. They were evidently not completed, on account of the confined space not permitting of further progress. It was from one of these cavities that the specimen exhibited was taken.

Here are two other small bits of comb from the small cavities spoken of. The cells are increased in number, but are less advanced than in the first piece. This (Pl. XIII. fig. 2), the smallest piece of comb, shows four cells in a rudimentary condition; the most advanced of these cells (and no doubt the one first commenced) is nearly hemispherical; attached to this is a second cell, rather less advanced, and in the interspace of these two cells are two others, presenting a still earlier condition. The smaller of these latter has its outer free portion nearly semicircular, whilst the inner half is formed by portions of the two adjoining cells, these portions presenting curves encroaching upon the small rudimentary cell. The partitions between the other three cells show a slight tendency to become flattened. Comparing this piece of comb with the piece to which I first drew attention, it will be seen that the diameter of each of these rudimentary cells is less than that of the more advanced cells. The most advanced of the four cells is already half-surrounded by the adjoining cells.

This piece (Pl. XIII. fig. 3), from the same great nest, is still further advanced. It consists of a comparatively deep cell (*a*)—still, however, nearly hemispherical—and five other cells in different stages of progress, enclosing about five-sixths of its circumference. Viewing this piece (exhibiting the foundations of six cells) in connexion with the other pieces exhibited, and, again, with a piece of comb in a still more advanced state, where all the cells are of one diameter, and all (except the outermost series) are hexagonal, it seems to me impossible to avoid the conclusion that the deepest and most advanced of the six cells was the one first formed; that the cell next formed was this one, which, you will perceive, is rather more advanced than the other cells surrounding the first one, and that this little shelf (*b*), with a very gently concave inner surface, was the last work of the insect; it is the commencement of the sixth cell.

The work here is somewhat rude and irregular, as compared with that seen in cells more advanced in condition. For instance, this (*c*), which from its state of advancement must have been the fifth cell commenced, unlike the other cells surrounding the first one, does not come in immediate contact with it; at least, the partition between cell (*a*) and cell (*c*) is double the usual thickness. I have already described how the first cells constructed form, as it were, a mere expanded portion of the previously formed stalk. This stalk is more or less irregular, and in this particular instance it is strengthened by a lateral pillar, on the summit of which the fifth cell is commenced. Again, the axes of the cells surrounding the first cell are not equidistant. The centres of the shallow little cavities, presented by the earliest condition of the cells, are more approximated than in those which are more advanced; but of necessity, if the work is continued, the centres must be gradually shifted as the work proceeds, until the whole of the cells surrounding the first one shall have attained their full diameter. Then, the diameters of all the cells being equal, the circumference of cell 1 must admit of six other (and only six other) cells being joined to it.

I have still other points to notice in connection with this particular piece of comb. Here the first formed cell (or rather *part* of a cell, for we see no perfect cells in any of these specimens) is purely circular in its horizontal section, whilst the second and third cells are separated by a flat partition. These are slight irregularities in the work, and I dwell upon them because I believe that it is only by bestowing close attention to such points that we shall arrive at any satisfactory solution of the problem furnished by the hexagonal form of the cells of these insects.

Lastly, I will notice, that notwithstanding the very small amount of work that has been bestowed upon these six rudimentary cells, there is still a small portion of another cell visible. This little shelf (*d*), which springs from the angle between two marginal cells, is clearly the commencement of a cell.*

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* The pieces of comb just described are undoubtedly the work of the neuter insects. Mr. Smith, our best authority for all that appertains to the Hymenopterous insects, thus describes the early work of the female wasp:—"She begins by making three circular saucer-shaped receptacles, in each of which she deposits an egg; she then proceeds to form other similar shaped receptacles, until the eggs first deposited are hatched, and the young grubs require a share of her attention. From the circular bases she now begins to raise her hexagonal cells—not building them up at once, but from time to time raising them as the young grubs grow." See Proc. Ent. Soc. Lond. 1858, p. 35.

From certain specimens before me of the early work of the female wasp, I will make a slight addition to the above. These specimens, being forwarded for the purpose by Mr. Stone, were exhibited by Mr. Smith at our last meeting (in February; see Proc. Ent. Soc. 1864, p. 2), and are now again before you for inspection. They have kindly been placed in my hands for examination since their first exhibition. Amongst these specimens is a single isolated cell, or rather a commencement of a cell—it being the first one constructed by the insect. It is in the form of a low, hollow cone, the pointed end being attached to a small stalk, and is about one-eighth of an inch in height, and of the same width at its opening. Under a magnifying glass it appears to be built entirely of glistening, whitish, silk-like threads, which I have little doubt are a secretion from the insect, all the threads being firmly attached together as if they had originally been of a glutinous nature. Of two other specimens, one shows three low, hollow cones, each cone united to two others, and at their junction having flattish partitions. The third specimen shows four such cones, with flat partitions between them. The largest of these cones scarcely exceeds the first isolated cone in size, and there are some which are decidedly smaller. Under a lens the work appears rather rude and irregular, the apices of the cones not springing from the same level, and the so-called flat partitions only in a rude manner sketching out the future hexagon. These cells differ from those formed by the neuters, later in the season, in being of smaller size, and in apparently having no admixture of foreign substances (such as masticated dead or rotten wood, which appears to be most commonly used) in their composition; and I cannot help thinking that the extreme economy of material which is apparent in the spring nest formed by the female wasp, not only in the formation of the cells, but likewise in that of their covering, has connexion with the nature of the material used. Almost simultaneously with the commencement of the cells, it appears that the nest-covering is commenced. At first it has the appearance of a miniature umbrella, serving to shelter the rudimentary cells. As the cells progress so does the thin covering, by additions to the free edge, until, when com-

I will now call attention to some pieces of comb of another species of wasp, the *Vespa orientalis*. These specimens may be seen in the British Museum. Here the cells, instead of being built of minute fragments of wood, glued together by a secretion from the insect, as in the case of the pieces of comb of the common hornet which I exhibit, are built of clay, and the work is extremely beautiful and true. Under the same glass shade are three slabs of comb of this Indian hornet (a large piece and two small slabs) ; one of the small slabs is fractured in parts ; the other is perfect, and this I will endeavour to describe, for if taken in connexion with what has already been said of the specimens exhibited, I think I shall then have directed your attention to some very important facts connected with the matter in hand.

This slab of comb is nearly round, rather more than two inches in diameter, and contains thirty-five cells in different stages of progress. Both surfaces of the slab are gently convex. All the cells form equilateral hexagons, excepting those which belong to the outer or marginal series. A few of the cells in the central part of the slab may be said to be complete, or very nearly so, having attained their full depth ; and from the centre towards the margin the cells are successively less deep. Those on the margin, however, vary considerably in their depth, or, we may say, in their state of progress. Many of them have attained about half their full depth, and most of these are, at the opening of the cell, nearly true hexagons ; each of them is in contact with four other cells, and each one of four of its sides thus forms a partition common to two cells. These sides meet so as to form true angles, but the two remaining sides of each cell, which as yet are not in contact with other cells, are less truly flat, and at their junction form a slightly rounded angle. Viewing these cells on the outer surface, we perceive that the imperfect angular form, which the cell has attained at its opening, rapidly disappears towards the base of the cell, which is rounded. Besides these half-formed cells, which have two free sides, there are two half-formed cells that are in contact only with three of the inner series of cells, and these two have three free sides each, which sides meet so as to form two slightly rounded angles at the outlet of

plete, it assumes a spherical form, but with an opening on the lowest part for the ingress and egress of the wasp. A second, and even a third covering successively follow, and are detached from each other. The largest of the nests exhibited by Mr. Stone is scarcely equal to a hen's egg in bulk, and the smallest is not larger than a medium-sized walnut.

the cell, which angles disappear towards the base of the cell, as in the other, much more common, form of half-constructed cells. The other cells of the external series are less advanced and show no trace of angles externally, the outline of the part not in contact with other cells being, in a horizontal section, in the form of a segment of a circle. These latter cells have not attained their full diameter.

I have now to refer to some other specimens which I exhibit; and, first, to two cells, which were constructed by a bee—*Osmia leucomelana.* They are formed of mud; and each cell is built separately. The female bee having deposited a small pellet of mud in a sheltered spot, between some tufts of grass, immediately commences to excavate a small cavity in its upper surface, scraping the mud away from the centre towards the margin by means of her jaws. A small shallow mud-cup is thus produced. It is rough and uneven on the outer surface, but beautifully smooth on the inner. On witnessing thus much of the work performed, I was struck with three points: 1st, the rapidity with which the insect worked; 2ndly, the tenacity with which she kept her original position whilst excavating; and, 3rdly, her constantly going over work which had apparently been completed; at every fresh addition of material brought up to the margin of the cell, the bee worked back again in the cavity which was already rendered smooth. To continue the cell, more material has to be sought for. It is added to the margin of the little cup first scooped out, and is wrought, by scraping, on the inner side; and here, again, it is certain that the bee does not entirely confine the work of her jaws to the additional material, but again passes them over the old work, and hence the part of the work already completed has a certain influence upon that which follows. The curves first formed have an influence upon those that follow, and, if continued, they would return again into themselves; that is to say, the cell would become a hollow sphere, but the tendency to this form is partially overcome by the fact that the cell has to be constructed by excavation, and by an insect which, when at work, is on the outside of it. The effect is, that it gradually passes from the spherical towards the cylindrical form, but never quite attains the latter, for the sides gradually close in, and ultimately the aperture becomes too contracted for the bee to insert her head and to carry on the work as before. Still fresh mud is added to the margin of the cell, but only to the inner edge, and this is continued horizontally, ring after ring of mud, till the cell is closed in by a lid; the lid is excavated and rendered concave on its outer or upper surface, and is convex and rough on its inner surface, and, in fact, is a simple repetition of the first-formed portion of the cell, a part of a hollow sphere; and if the work proceeded beyond this point, there can be little doubt that this lid of a cell would become the bottom of another similar cell, and thus we should have the cells joined end to end, and with a common straight axis, as we see in the cells of certain other bees—*Megachile* for instance; here, however, the cells are deposited in cylindrical burrows made in the ground, and the cells themselves are cylindrical. I have witnessed the construction of the first part of the cell of the *Osmia*, and I have seen cells in all states of progress from that part to their completion. The completed *Osmia* cell strongly reminded me of the isolated cells built by the hive-bee for the queen-bee larva; the general form is the same to this extent,—they are both hemispherical at the base, and gradually approach the cylindrical form towards the mouth of the cell.

I have still one other form of cell, to which I wish to direct your attention. These two cells, like those of the *Osmia*, are constructed of mud, but the insect that formed them (a species of *Eumenes*) belongs to the wasp tribe. Whilst the *Osmia* is a short stout insect with short legs, the *Eumenes* is slender and has long legs. The cell of the *Osmia* would be completely filled by the pupa of the insect reared in it; but that of the *Eumenes* is much larger when compared with the size of the insect that constructed it. This difference in the proportionate size of the cells has, no doubt, reference to the kind of food which has to be stored up for feeding the larva. Furthermore, these cells differ from those of the *Osmia* in being almost perfectly spherical. They remind one of certain water bottles, and, like them, have a short neck, through which is the opening into the nest. The opening is very small, but I have little doubt would permit the insect to enter the cell; but, on the other hand, I much doubt whether she could perform the whole of the work of its construction from the outer side. I believe, indeed, that in executing the latter part of the work, at least, the insect was inside the cell. However this may be, here is a cell, the foundation of which was laid down in segments of circles of much larger size than those seen in the cell of the *Osmia*, and, in connexion with this, we have the fact, that the comparatively long legs of the *Eumenes* would give it the power of a far greater stretch, supposing that her work was com-

It is extremely difficult to observe the cilia which lie at the bottoms of the furrows (*mf*). Wallengren (*l.c.*) ascribes to them the duty of carrying lengthwise of the furrow to the lower margin of the palps the minute particles that may fall between the ridges. But Siebert ('13) thinks they lead in the opposite direction.

In the event that any particles get past the palps they may still be rejected at the mouth. A strong compression of the lips will force them outward to the edge of the lips, where they encounter the cilia directed backward (Figs. 3 and 4, lower margin) and are carried to the edge of the palps and dropped into the mantle chamber.

The outer surfaces of the palps and lips have as their function the removal of particles from the mantle chamber (Fig. 4).

McAlpine's (*l.c.*) observations upon the movements of detached parts led him to conclude that the palps and gills have nothing to do with feeding, and that they are concerned only with carrying away foreign material. But Wallengren's (*l.c.*) conclusions are based upon far more careful and logical experiments, and Siebert's (*l.c.*) recent paper on the epithelium of Anodonta is of a confirmatory nature.

Observations.

The ciliary currents may be observed quite readily on a mussel from which the shell and mantle of one side have been removed, or on detached parts, which, as stated, continue to exhibit ciliary activity for a long time. Small quantities of carmine, indigo, or other nearly neutral coloring matter may be dropped upon the part to be studied, and their behavior noted. Care must be exercised in the amount of water used. The less water the better, within limits, for in a large amount of water currents may obscure the action of the cilia. The surface of the organ must be level in order to offset gravitational disturbance. A small piece of any ciliated organ, when placed in a watch glass with water and a very little color, will show under low power both the cilia and their currents in great detail.

The Ciliary Streams.

The figures will show more clearly than description the course of the streams of material collected from the water. All the ciliary currents of the inner gills (Figs. 1, 2, 4, 6, and 7) are seen to be directed downward. When they reach the lower edge of the gill they pass around the points of the lamellæ to the under side. Here the lamellæ of the two faces of the gill form an inverted trough (Fig. 7, *tr*) in which the particles small enough to be used as food may be carried to a point just above the labial palps (Figs. 1 and 2, *X*). At this point they accumulate in strings of mucus until their weight causes them to fall into the mantle chamber, or into the trough formed by the upper margins of the palps. This depends upon the desirability of the material for food, or rather upon the presence or absence of unfavorable stimuli, and is probably regulated by reflexes, since the palps are quite motile, even after being severed.

The ciliation of the outer gills tends upward (Figs. 1 and 6). When particles carried upward by their inner surfaces reach the top, they are passed over to the inner gill, and thence to the point described above. But the gleanings obtained by the outer surface of the outer gill pass over to the mantle at the line of their attachment (Figs. 1 and 6). All material transmitted by the outer gill and collected by the uppermost part of the mantle is removed forward by the latter to a point just above the attachment of the palps to the mantle and body wall. So long as the upper edge of the palps remains applied to the mantle this material passes into the trough between the palps, backward around the line of attachment of the two palps, then forward again between them (Figs. 3 and 4). In case of an unfavorable stimulus the palps are withdrawn from the mantle at this point the material glides past them and is carried downward and backward by the cilia of the lower part of the mantle to the region of the excurrent siphon (Fig. 1). All the cilia of the lower part of the mantle are directed toward the posterior. So are those of the epithelium of the lower body wall. Their function is that of collecting particles to be thrown out. A small portion of the body wall, near the upper margin, is ciliated like the same portion of the mantle, and must be concerned with the collection of food.

From the foregoing account and from the figures it is evident that the region of the labial palps is the center toward which all the ciliation of the upper part of the mantle chamber tends. All material gathered by both gills and by the dorsal part of the body epithelium and mantle must finally reach one of the three adjacent points—(1) the mantle just above the palps, (2) the body wall just opposite the first point, or (3) a point on the edge of the inner gill just above the labial palps. All these are within easy reach of the palps (Figs. 1, 2, 4, and 6).

No one, to my knowledge, has succeeded in inducing a mussel to behave normally, after the shock of removing parts of the shell and mantle in order to observe the palps at work. But I have repeatedly obtained the reactions which occur. When the palps lie in contact with either body, mantle, or gill, their collections of material pass between the palps and mouthward. Otherwise such material is carried on down by the several structures and discarded. The fact that the upper margins of the labial palps adhere to each other and form a trough (Figs. 4 and 6) makes it possible to reach at least two of the three sources of supply simultaneously.

Since we have the mechanism for such a method, and since the reactions, though fragmentary and under abnormal conditions, are of a confirmatory nature, we may safely infer that the labial palps do actually accept or refuse food, either through reflex stimuli or in response to volition.

The Function of the Mucus.

The entire epithelium touching the branchial chamber is abundantly supplied with glands which secrete a mucous substance (Siebert, *l.c.*). The mucus envelops and binds together in strands the material to be transported by the cilia. This is particularly true of those particles which are of a very distasteful nature. That this secretion is dependent on local reflexes is quite evident from the fact that it may be stimulated in an organ entirely severed.

It is this collection of food in a film of mucus, which makes possible the mechanism of the furrowed surface of the labial palps. If each particle were manipulated independently, it would tend to eddy back and forward between the opposing streams of cilia, and considerable confusion might result. But a strand of material spans the summits of several ridges, and while touching cilia that lead in both directions, it obeys the ciliary streams which lie uppermost and exert the greater force upon it.

Conclusions on the Function of the Ciliary Currents.

The surfaces of the gills and of the upper part of the mantle, and the contiguous faces of the labial palps, in fact, nearly all the upper parts of the mantle chamber, have for their general purpose the carrying of food to the mouth. The lower part of the mantle chamber, upon which the heavier fragments are likely to fall, are concerned principally with removing undesirable matter from the animal.

THE SELECTION AND REJECTION OF FOOD PARTICLES.

Observers have differed widely in their notions of the ability of the mussel to select its food. To me it is evident that there are, to summarize, four points where such choice is exercised:

(1) The labial palps, at the upper margin.
(2) The labial palps, on the furrowed surfaces.
(3) The mouth.
(4) The incurrent siphon.

As to the last, it is surrounded by a row of pointed, fleshy papillæ, having a resemblance to plant structures. These have two sensory functions—tactile and gustatory; for upon being disturbed mechanically they are withdrawn into the shell, while a continued teasing, or a strong chemical stimulus results in the closing of the shell, or perhaps only the siphons.

It is true that some material of no food value finds its way into the alimentary canal. But the quantity is far smaller than if no selection were made, and is of a harmless nature. All distinctly injurious substances are rigidly excluded.

That which has been rejected at the mouth, palps, or gill accumulates upon the lower posterior margin of the mantle or body wall, along with the collections made by these parts themselves, and is here massed in clots of mucus. When this has attained considerable size the animal ejects it with a rapid current of water, set in motion by a quick contraction of the adductor muscles and closing of the shell (Figs. 1 and 2, *r*).

The Rate of Siphoning.

An effort was made to determine the rate at which water is siphoned through the mussel. If this can be done it will contribute to several quantitative studies relative to the feeding habits, and that of the effect of temperature and other conditions upon the activity of the cilia.

But it is very difficult to attach apparatus for making measurements to the siphons of the animal. Intimate contact must be made to avoid leakage and a high per cent. of error. Such contact irritates the mussel, so that it does not behave normally.

In only one mussel did I succeed in obtaining what seemed a normal circulation of water, when under this annoyance. This was done by placing a short piece of soft rubber tubing in the excurrent siphon. Into the end of this was thrust a calibrated glass tube, having a capacity of 2 c.c. between two given marks. The point of a pipette containing neutral coloring matter was thrust into the rubber just outside the siphon. The mussel with this simple apparatus was put into an aquarium near the lake, where the water could be changed frequently and the lake conditions maintained. A touch upon the pipette released a drop of coloring matter into the tube, where it encountered the stream flowing from the excurrent siphon.

This individual was a *L. luteolus* weighing 200 grams with the mantle chamber filled. It required five seconds for the pigment to pass between the two marks upon the tube, whenever the incurrent siphon was opened fully. The reading was repeated a number of times at intervals, with the same result.

While these are but meager results, they give at least an idea of the volume of water siphoned. At the above rate there are siphoned 24 c.c. per minute, 1,440 c.c. per hour, or 34,560 c.c. per day. To filter a liter of water would require 42 minutes.

Digestion.

Digestion fluctuates more in the case of mussels than does their feeding. That is, the animal continues to feed regardless of appetite; but the degree with which the food so ingested is really made use of seems to depend upon the relation of supply and demand. At times nearly all the intestinal contents are found to be at least partially digested; while again much material is found, even in the rectum, in perfect preservation, and often the fæces themselves contain forms which are apparently unaffected. Hence we may conclude that appetite fulfills its function by the control of the secretion of the digestive juices, without the voluntary regulation of the food supply.

The Crystalline Style.

The literature on the lamellibranchs is particularly rich in speculations concerning the function of the crystalline style; but I cannot forbear adding a word here parenthetically on the subject, by calling attention to the excellent work done by Mitra ('01) upon it. He reviews all the previous theories and repeats the experiments, extends them, and brings physiology, chemistry, and comparative morphology to bear upon the matter, so that there seems to be no way of escaping his conclusion that the style is a digestive ferment which converts starch into sugar. The previous hypothesis of Gegenbaur, that it is a secretion of enteric epithelium, he holds to be true, but says that this does not account for its existence. Against Balfour's notion that the style is a rudiment of a radular sac he brings six weighty proofs, and dismisses with two objections each the theories of Claus and Sedgwick, that it is an excretion product and a reserve of nutriment, respectively.

In two minor particulars my observations do not agree with those of Mitra. (1) In an experiment upon the renewal of the style he concludes that it appears and disappears *periodically*. But from the description of his experiment we find that the water and food supply were renewed at regular intervals, whence the periodicity. In a similar experiment of my own the crystalline style was found to disappear only with the lack of food, and to be regenerated only when food was supplied, regardless of time. Then too, as long as the food supply is abundant the style is never wanting. In all mussels freshly removed from the lake it was found to exist. In all mussel freshly removed from the lake it was found to exist. In these matters the work of Haseloff ('88) also confirms my point.

Hence the food supply must be a factor in its secretion. As it is dissolved when food is lacking, and as it is a proteid, why is not Sedgwick's theory as to its being a reserve food supply also true?

(2) The presence in the core of the crystalline style of cells similar to those found in the liver epithelium leads Mitra to conclude that the liver is the probable origin of the structure. This also does not seem well substantiated, especially in species where the style is found in a diverticulum. No channel for the passage of a secretion from the liver to the seat of the style has been discovered, and the ciliation of the stomach and intestine forbids their aiding in its transmission.

Since the publication of the above paper Grave ('03) has suggested in his work on the oyster that the crystalline style may perform the duty of preventing coarse particles from passing through the digestive canal. In fresh water mussels I can see but one way in which the style may attend to that function—by digesting the said particles. There are at least two objections to this explanation for fresh water mussels (1) As we have seen, the animal is well protected against the entrance of such particles. (2) In case they were admitted to the stomach but kept out of the intestine, they would accumulate in the stomach, for it is not equipped with either a muscular or a ciliary system by which these could be expelled through the mouth. Then too, the mouth is no larger than the intestine and no more capable of receiving them. The largest body I have seen in the alimentary tract was a fragment of *Oscillatoria* (or similar form) measuring 1.5 mm. in length.

Food Materials.

No one but Zacharias ('07) seems to have undertaken a detailed examination of the contents of the alimentary tract of the freshwater forms, so I give the results of a purely qualitative examination. In marine mussels it is said that the food consists almost altogether of minute plant forms, and of these almost all are Diatomaceæ. In the mussels which I examined I found a somewhat different condition. In the first place there is a little higher proportion of animal food present. Living animals are found but rarely, and most of these are apparently living transiently upon the contents of the tract. But the mussel does